



## Original investigation

Context-specific tool use by *Sus cebifrons*Meredith Root-Bernstein<sup>a,b,\*</sup>, Trupthi Narayan<sup>c</sup>, Lucile Cornier<sup>d</sup>, Aude Bourgeois<sup>e</sup><sup>a</sup> UMR Sciences pour l'Action et le Développement, Activités, Produits, Territoires, INRA, AgroParisTech, Université Paris-Saclay, F 78850, Thiverval-Grignon, France<sup>b</sup> Institute of Ecology and Biodiversity, Santiago, Chile<sup>c</sup> Local and Indigenous Knowledge Systems, UNESCO, Paris, France<sup>d</sup> Master 2 Applied Ethology, University of Paris 13, Paris, France<sup>e</sup> Ménagerie du Jardin des Plantes, Muséum National d'Histoire Naturelle, Paris, France

## ARTICLE INFO

## Article history:

Received 15 February 2019

Accepted 20 August 2019

Available online 21 August 2019

Handled by Sabine Begall

## Keywords:

Tool use

*Sus cebifrons*

Suidae

Nest building

## ABSTRACT

Tool use has been reported in a wide range of vertebrates, but so far not in Suidae (the pigs). Suidae are widely considered to be “intelligent” and have many traits associated with tool use, so this is surprising. Here, we report the first structured observations of unprompted instrumental object manipulation in a pig, the Visayan warty pig *Sus cebifrons*, which we argue qualifies as tool use. Three individuals were observed using bark or sticks to dig with. Two individuals, adult females, used the sticks or bark, using a rowing motion, during the final stage of nest building. The third individual, an adult male, attempted to use a stick to dig with. Stick and branch manipulation was observed in other contexts, but not for digging. Our observations suggest the hypothesis that the observed use of stick to dig with could have been socially learned through vertical transmission (mother-daughter) as well as horizontal transmission (female-male). When used by the females, it altered their digging affordance, and had a specific placement in the nest-building sequence. In addition to its context-specificity and its role in a functional sequence, the observed tool use is distinguished by an ambiguous function or effectiveness as a digging behaviour, and the participation of the male in a female action pattern. Observations of unprompted tool use represented for the first time in a phylogenetic family are rare. These open new possibilities for research on tool use and social learning in Suidae.

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## Introduction

Tool use has been reported in a wide range of vertebrates (e.g. Whiten et al., 1999; Hunt and Gray, 2004; Breuer et al., 2005; Krützen et al., 2005). Tool use may be defined as “the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium ... via a dynamic mechanical interaction, or (2) mediating the flow of information. ...” (St. Amant & Horton, 2008). Here we report on behaviours that fit this definition of tool use observed for the first time in Suidae, by *Sus cebifrons*. *Sus cebifrons*, the Visayan warty pig, is native to the Philippines, and is critically endangered (Oliver, 2008; Przybylska, 2014). Domestic pigs (*Sus domesticus*) are considered to be “intelligent” animals (Mendl et al., 2010; Marino and Colvin, 2015), with many of the

cognitive and behavioural traits associated with tool use, so it may be surprising that pigs are not known to use tools.

Tool use has often been observed in extractive foraging contexts and may also be related to nest-building. For example, capuchin monkeys (Moura and Lee, 2004), chimpanzees (Whiten et al., 1999), orangutans (Fox et al., 2004) and New Caledonian crows (Hunt, 2000) use tools during extractive foraging. Extractive foraging is thought to require some form of cognitive “representation” of visually unavailable food sources, along with the potential use of objects as bodily extensions to perform the extraction, and as such may lay the cognitive groundwork for tool use (Van Schaik et al., 1999; Ottoni and Izar, 2008). Many species that carry out extractive foraging do not use tools, although both have been linked to the evolution of intelligence, suggesting a set of related capacities (King, 1986). However nest-building is not usually considered a form of tool use, though it may involve manipulating natural materials to alter the physical properties of other materials, until a protective, stable structure is formed; nest-building capacity has also been related to the evolution of tool use (Fruth and Hohmann, 1994; Healy et al., 2008). Suidae are both extractive foragers and nest-builders.

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Wild pigs are omnivores and extractive foragers of roots, eggs, fruits, seeds, mushrooms, and so on (e.g. Skinner et al., 1976; Ghiglieri et al., 1982; Leus and MacDonald, 1997). Pigs frequently collect objects with their mouths and engage in exploratory “investigatory chewing”, in the course of foraging and nesting behaviors (Studnitz et al., 2007; Allwin et al., 2016). Wild pigs are playful, and “playful digging”, throwing objects into the air, and chasing an individual that has obtained an “interesting” object have been reported in Suidae (Frädrich, 1974). Pigs, unlike other ungulates, also build nests. Nest building in wild pigs takes two forms: farrowing nests and loafing beds (MacDonald, 2000; Mayer et al., 2002). Constructing farrowing nests in particular involves the manipulation of materials and objects. Farrowing nests are generally oval-shaped depressions lined with leaves, grasses or other vegetation (Allwin et al., 2016; MacDonald, 2000; Mayer et al., 2002). Loafing beds may sometimes also be lined, but are less elaborate (MacDonald, 2000; Mayer et al., 2002). The presence of nesting material stimulates farrowing nest-building behavior during the reproductive periods in spring and fall, when prolactin levels are high in reproductive female pigs (Arey et al., 1991). Farrowing nest construction has been described as a typical action program released by a sequence of internal conditions and external cues, and is modifiable by learning through individual experience (Jensen, 1989; Thodberg et al., 1999; Sutherland-Smith, 2015). In the wild, farrowing nests are built by pre-parturition sows (Mayer et al., 2002; Sutherland-Smith, 2015; Allwin et al., 2016; Veit et al., 2017). Pigs’ extractive foraging, object manipulation, playfulness, and nest-building make them candidates for tool use, although their lack of digits or beaks allowing for a finely controlled grasp may limit their expression of such behaviour. To our knowledge there is no literature on tool use in pigs.

These same traits and pigs social structures also make them candidates for innovations and their social transmission. Young of the year form a social unit with the mother, while in most Suidae, adult males are solitary except during the breeding period (Dardaillon, 1988; Sutherland-Smith, 2015). However, wild males of *Sus cebifrons* are reported to live within a family unit, including a mated female and their young, throughout the year (Przybylska, 2014). Innovations in object manipulation can occur in a wide range of behavioral contexts (Kummer and Goodall, 1985; Reader, 2003). Social learning can take many forms, with different aspects of the original behavior—i.e. its informational content, motor patterns, object of manipulation or interaction, context, and goal—transmitted via different mechanisms, some of which are available to particular species’ cognitive abilities or in certain situations, and others not (Laland, 2004; Galef and Laland, 2005; Rendell et al., 2011; Heyes, 2012). In the only report of innovation in pigs that we are aware of, *Sus scrofa* were observed to have innovated food washing behaviour at the Basel Zoo, but the mechanism of transmission (if any) was not observed (Sommer et al., 2016). Social learning in pigs has been relatively little studied (e.g. Nicol and Pope, 1994; Held et al., 2000), but shows that pigs can use cues from conspecifics to direct foraging behavior. Oostindjer et al. (2011) identify a combination of local enhancement and stimulus enhancement as underlying piglets’ learning from their mothers about novel food sources. Sommer et al. (2016) similarly suggest that stimulus enhancement could have been the mechanism of social learning, if social learning took place in the acquisition of the observed food washing. Stimulus enhancement can support the acquisition of tool use behaviours (e.g. Zuberbühler et al., 1996).

The present studies were designed in response to an accidental observation, by one of the authors, of an apparent tool use event at the Ménagerie in Paris. We will refer to what appears to be tool use by the synonymous construction “object manipulation” until having presented all of our evidence at the end of the paper. In October 2016 one of the authors (MR-B) made the following notes

after observing a female Visayan warty pig (*Sus cebifrons*) digging in a nest: “She would deposit some leaves, move them to a different spot on the [nest] mound, and dig a bit with her nose. At one point, she picked up a flat piece of bark about 10 cm x 40 cm that was lying on the [nest] mound, and holding it in the middle in her mouth, used it to dig, lifting and pushing the soil backwards, quite energetically and rapidly. The digging motion was repeated six or eight times.” Enquiries to the keepers responsible for the Visayan warty pigs indicated that they were not aware of any behaviours fitting the definition of tool use by them. We also made enquiries with other zoos with Visayan warty pigs, which also did not report this behavior. We consequently set up a series of observations under different conditions in an attempt to (1) verify the initial observation, which would be the first report of tool use in Suidae, and (2) determine under what conditions and by which individuals these behaviours are carried out.

## Material and methods

### Study site

The study was carried out at the Ménagerie of the Jardin des Plantes, Paris, France, a member of the European Endangered Species Program (EEP) of the European Association of Zoos and Aquariums (EAZA). Across participating zoos, the EEP had 1387 Visayan warty pigs in 2015. The Visayan warty pig enclosure at the Ménagerie, holding 4 pigs, is an 80 m<sup>2</sup> fenced area covered in mulch and with some large tree trunks, along with a 4.5 m<sup>2</sup> hut. The male is kept with the females year-round, which appears to be the natural social system for wild Visayan warty pigs (Przybylska, 2014).

Permission for the studies was obtained from the Ménagerie. All applicable institutional ethical and animal welfare guidelines for the care and use of animals were followed.

### Subjects

The Ménagerie has a female born in captivity in 2007 (“Priscilla”), a male born in captivity in 2009 (“Billie”), and their two unnamed female offspring born in 2012. As a general methodological note, Billie and Priscilla were clearly distinguishable individuals, but although the two adult female offspring could be distinguished during each experiment by comparison, slight changes in their appearances across years as well as change in observers across years means that we are not sure that female offspring 1 is the same individual across Experiments 1 and 2. In Experiment 3 we established a key to identify each and gave them names, Antonia and Beatrice, in order to ensure consistency across observers.

### Study 1

Following the initial observation MR-B visited the Visayan warty pig enclosure at the Ménagerie on an *ad hoc* basis for the next six weeks multiple times per week, at different times of day in an attempt to repeat the observation and obtain photographic evidence. However, no further instrumental object manipulation was observed during visits through December 10, 2015. She observed that the same piece of bark originally used as a digging tool remained visible. However, the piece of bark was observed at different positions within the enclosure, always lying next to a recently created nest pit (Fig. 1). As the keepers did not enter the enclosure during this period, the movement of the piece of bark can only reasonably be attributed to the Visayan warty pigs. Its consistent position next to a nest pit with signs of recent digging allowed us to form the hypothesis that the piece of bark may have been fetched and used as a digging instrument by at least one of the individuals



**Fig. 1.** Far left, the mother Visayan warty pig, Priscilla, (indicated with arrow) immediately after using the piece of bark to dig in the nest pit indicated by the dotted oval (behind the two individuals). Center, the piece of bark (indicated with arrow) was later observed next to the new nest pit shown circled. Far right, the piece of bark was subsequently observed next to a new active nest pit. It was not observed in the enclosure after this occasion. Photos © MR-B.

on more than one occasion. The piece of bark eventually disappeared. The creation of new nest pits in the enclosure also declined during this period.

At this point we did not know in what contexts instrumental object manipulation might occur, although it was linked to manipulating the soil, through digging or rooting activity. Since nest making only occurs at six-month intervals, we decided to focus first on extractive foraging, in the form of digging and rooting, as a possible instrumental object manipulation context. We hypothesized that the digging behavior and associated instrumental object manipulation could be stimulated by increased foraging. To test this hypothesis we set up structured observations under enriched foraging conditions (Reader and Laland, 2003).

#### Methods, study 1

LC implemented two feeding enrichment conditions in an attempt to stimulate increased foraging-related digging, which we predicted would result in episodes of use of tools for digging. The four Visayan warty pigs have constant access to their outdoor enclosure covered in mulch. Normally the pigs are fed twice a day, at 11:30 and 14:15, with fruits and vegetables distributed in the enclosure and grains in the hut. The two feeding enrichment conditions consisted of (1) a pile of dry leaves next to the fruits and vegetables in the enclosure, and (2) the fruits and vegetables mixed into a pile of dry leaves in the enclosure. The control condition consisted of the normal feeding procedure, without any added leaves. Sticks were also provided in the enclosure in all conditions to ensure that instrumental object manipulation would be possible. The three conditions were rotated, one condition per day, for 9 non-consecutive days during November and December 2015. During this period no nest-building behaviour was observed. Focal Behavioural Sampling was used, focusing on each individual in turn for periods of 5 min. The total observation period each day consisted of the duration of each feeding session (of variable length determined by the amount of time spent eating by the pigs) and for 1 h after each feeding session. The observer recorded the following variables: duration of feeding, the number of rootings into the mulch and the number of rootings into the leaves, and number of object manipulation events that qualified as instrumental object manipulation (i.e. tool use according to the definition used in the Introduction, which could be readily observed in situ, see Ethogram (Table 1)). The rooting action of the pigs consists of probing the substrate with their snouts or pushing the material forwards, away from them. This motion differs significantly from the observed instrumental object manipulation, in which the digging motion with the piece of bark held in the mouth was used to

**Table 1**

ANOVA of the factors affecting total time spent rooting in the leaves and enclosure substrate, combined. Condition refers to the experimental condition, interval to during feeding or after feeding. P values in bold are significant.

variable	df	Sum sq.	Mean sq.	F	p
pig	3	3	207	2.541	0.09
condition	1	1	1120	41.211	<b><math>5 \times 10^{-6}</math></b>
interval	1	1	6991	257.345	<b><math>4 \times 10^{-12}</math></b>
residuals	18	489	27		

push the soil backwards, to one side of the individual, similar to a paddling or rowing movement.

Monte Carlo permutation tests were used to compare times across conditions for each individual. We further used Engauge Digitizer (see <http://markummitcheil.github.io/engauge-digitizer/>) to extract data on the number of rooting events from summary graphs created by LC, and performed an ANOVA on this data to look at factors affecting number of rooting events across 'pigs' as a group, in R 1.0.136 (R Core Team, 2017).

#### Results, study 1

The duration of feeding did not differ across enrichment conditions in any of the individuals (male (Billie): Monte-Carlo,  $\chi^2 = 1.30$ ,  $p = 0.69$ ; mother (Priscilla): Monte-Carlo,  $\chi^2 = 1.88$ ,  $p = 0.42$ ; Female offspring 1: Monte-Carlo,  $\chi^2 = 1.58$ ,  $p = 0.48$ ; Female offspring 2: Monte-Carlo,  $\chi^2 = 0.45$ ,  $p = 0.81$ ). An ANOVA revealed that there was no significant difference in rooting events between pigs,  $F_{(3,23)} = 2.541$ ,  $p = 0.09$ . There was a significant difference across conditions,  $F_{(1,23)} = 41.211$ ,  $p = 5 \times 10^{-6}$ , as well as across intervals (during feeding or after feeding),  $F_{(1,23)} = 257.345$ ,  $p = 4 \times 10^{-12}$ . Thus across all individuals ('pig' as a factor), significantly more rooting occurred during feeding in the two conditions with leaves, but there was no difference in the number of rooting actions between conditions during post-feeding observations (see Table 2).

Although the pigs were observed to carry leaves and branches around in their mouths, a form of object manipulation, no instrumental object manipulation events were observed during or after feeding. Since we had been interested in the relation between rooting or digging and instrumental object manipulation, in this experiment we did not quantify object manipulation events in general. Non-quantified observations of object manipulation, however, revealed that the pigs collected the leaves and carried them from place to place, to line nest pits (Fig. 2). We observed that the Visayan warty pigs also picked up sticks in their mouths and carried them around. In at least one instance, one individual made typical forward-oriented rooting movements in a pile of leaves with its nose while holding a stick in its mouth, although whether the stick



**Table 2**

Ethogram of behaviours recorded in Study 3. Tool use here is defined with reference to the goal of this study and is of course not the only possible form of tool use by pigs. Where there are multiple forms that the behaviours may take, a detailed description was recorded in the field notes. The objects manipulated and the interactants were also noted.

	Description
Digging	Moving earth, mulch or leaves with the feet
Rooting	Moving earth, mulch or leaves with the snout
Kicking soil with hind feet	Moving earth, mulch or leaves by kicking it backwards with the hind feet
Moonwalking	The pig walks backwards while dragging the feet so as to build up earth, mulch or leaves into a mound or wall around the nest pit
Object manipulation	Handling, carrying, holding of an object in the mouth
Instrumental object manipulation	Holding a branch or bark in the mouth and making a rowing motion with the head such that the branch or bark contacts and displaces some soil, mulch or leaves Observationally meets the key requirements for tool use: exertion of control over an external object leading to alteration of physical properties.
Attempted instrumental object manipulation	Holding a branch or bark in the mouth and making rowing motions of the head in which the branch or bark fails to contact or displace the substrate, or the grip on the branch or bark is repeatedly adjusted before contact or after aborted contact with the substrate
Agonistic behaviour- chasing	One pig moves rapidly towards another, who retreats, often with threat display by the approaching pig
Agonistic behaviour- biting	One pig bites another usually in the context of a threat display by at least one of the two
Agonistic behaviour- threatening	One pig makes an intention movement to chase or bite the other, may vocalize, and is highly aroused and oriented towards the pig being threatened.
Subordinate behaviour- avoidance	Avoidance, including retreat or moving away, halting before approach, remaining in another pig's blind spot, and running away when chased were common forms of subordinate or submissive behaviour
Walking	Walking pace
Running	Trotting or galloping pace
Play behaviour	Any of the above behaviours, especially object manipulation, chasing and running, or others, when performed with the high energy, exaggerated movements, and incomplete sequences typical of play behaviour. For example, twirling while holding leaves in the mouth, or holding leaves in the mouth and shaking them in another pig's face. Often performed with another pig who responds with play behaviour.



**Fig. 2.** Adult female Visayan warty pig, carrying leaves to line a nest pit. Photo © LC.

assisted in the activity is not clear (Supplementary Material). This movement was also different from the digging-paddling movement observed with the bark used in the original observation.

#### Discussion, study 1

Although leaf enrichment during feeding led to increased rooting, and anecdotal manipulation of leaves and branches, we were not able to stimulate instrumental object manipulation during or following feeding. From this we concluded that rooting as a form of extractive foraging was not related to instrumental object manipulation in the Visayan warty pigs.

#### Study 2

Following Study 1, we hypothesized that the instrumental object manipulation for digging occurred only during farrowing nest construction, which is the behavioural sequence in which it was originally observed. We thus made further observations in 2016, during the nesting period in October.

#### Methods, study 2

Between 13-10-2016 and 27-10-2016, TN observed the Visayan warty pigs in an effort to determine in what behavioural

sequences instrumental object manipulation might occur. Observations started between 16:00 and 16:30, were carried out for between 90 and 120 min, and ended at closing time (18:00), being the period when nest construction was most common. Total observation time was 1470 min. The animals were visible at all times when they were in the enclosure, except when they went into the hut, mainly when it started to rain. Focal animal sampling of the entire group of pigs focused on observing digging with the stick. The mother, Priscilla, was prioritized since she appeared to be most active in the nest building process. Since there was a clear field of vision, the focal sub group involved the other two females when possible and lastly, Billie the male. Instrumental object manipulation was the focal event and each instance of this behavior was recorded with a video camera and notes were taken. Whenever the movements of the pigs appeared such that they might pick up a stick or piece of bark with their mouth, recording was started. The camera was hand-held to enable the researcher to move around the fence easily to get the best possible view of the behavior. The videos were not used for subsequent data recording, only as an attempt to provide proof of tool use. The footage included in the Supplementary Material is unedited.

#### Results, study 2

We observed instrumental object manipulation for digging by the adult female Priscilla and one of her daughters on 4 occasions (3 instrumental object manipulation events by Priscilla and 1 by one of the offspring), and video evidence was collected (Fig. 3; see videos in Supplementary Material). Different sticks and pieces of bark were used on each observed occasion.

In addition, the adult male, Billie, attempted to use a stick that one of the offspring had been using for digging on 24-10-2016. TN reported “one of the females again started to dig with a stick. . .one or two times, after which she abandoned the stick and went off to look for more leaves. Billie then investigated the stick and carried it off in his mouth, walking about the fence for a while before dropping it. After some time, he picked up the stick and attempted a rather clumsy digging action.” See also video footage in Supplementary Material.



**Fig. 3.** Frame captures of video of one of the adult female Visayan warty pigs (Priscilla), using a piece of bark as a digging tool, 2016. For the video, see Supplementary Material. Images © TN.

The instrumental object manipulation for digging was integrated into the nest-building behavior of the females on all occasions when the instrumental object manipulation was observed. In a typical sequence, first, the female pigs worked simultaneously at the same site to dig a depression and carefully arrange fresh and dry leaves in it. After this, additional earth was put into the nest, by shoveling with the snout, kicking backwards with the feet, and instrumental object manipulation as described above. The instrumental object manipulation was only observed at this stage in nest building, at the end of the day, and when there were few visitors at the enclosure.

#### Discussion, study 2

We were able to confirm the original observation of instrumental object manipulation, implying that this was not a one-off event, but a part of the pigs' behavioural repertoire. Moreover, a second female was observed to carry out the same behaviour, and the male appeared to attempt to carry it out. The results of these observations suggest that instrumental object manipulation occurs within the behavioural sequence of nest-building. Moreover, instrumental object manipulation appears to occur at a specific stage in the nest-building, at the end of the process. We also observed a range of stick shapes and bark pieces used to dig with. We note that this is in contrast to the initial observation of a single piece of bark being repeatedly moved to nest sites (though whether it was repeatedly used to dig with cannot be known). The fact that the sticks and pieces of bark used to dig with in the present study were not reused, or moved between active nesting sites, may reflect our qualitative assessment that they were not well-shaped to act as digging tools. This led us to speculate that the pigs may prefer, or be more successful in using, sticks and bark pieces that are well-shaped for digging and easy to grip.

#### Study 3

A lack of comparative data on group nest building in Visayan warty pigs in the wild, or any other Suidae, raised the question of how group nest building is structured, and how the use of the tool for digging in the nest fits into the nest-building action sequences and social dynamics. Following Study 2, we hypothesized that (1) Access to sticks that are easy to grip and have a flat area good for pushing mulch might increase instrumental object manipulation by all individuals; (2) Frequency of instrumental object manipulation may be related to social dominance, with the more dominant individuals controlling access to the tools; (3) instrumental object manipulation occurs only in a specific step of nest building, towards the end of the process. To test these hypotheses, we provided various novel spatulas as digging tools to the pigs during the following nest building season, and observed their social interactions and nest building sequences.

#### Methods, study 3

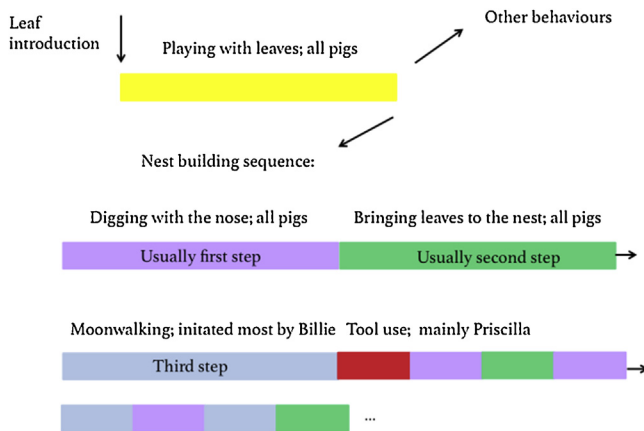
We carried out structured observations from 16:45 to 17:45–18:00 (when the zoo closed) every day between 23-03-2017 and 6-04-2017, corresponding to the time of day and period of the season in which nest building and instrumental object manipulation take place, according to Study 2. The total observational time was 840 min. Observations were carried out simultaneously and independently by TN and MR-B. Although we intended to carry out continuous observations of two pigs each, their behaviours were highly repetitive and interactive and in practice both observers took notes on all four individuals. We took continuous notes in order to characterize action sequences in their entirety. At the end of the study the notes of each observer were compared. There were no divergences in how we identified behavioural events, and only minor divergences in start and stop times for each behaviour. Since we were ultimately not able to run statistical tests on the event or duration data, we did not carry out a quantitative inter-rater reliability test on that data.

We provided the Visayan warty pigs with 4 wooden or bamboo spatulas of differing designs. Each one was provided in the enclosure for three sequential days and then removed by the keepers, and between 4–7 April all four were provided together. Dry or fresh leaves were also regularly added to the enclosure at the beginning of the observation period whenever previously available leaves had been used up or disappeared.

We recorded behavioural events, their start and stop times, and qualitative description e.g. of the object of the behaviour. We recorded digging, rooting, and a behaviour we called 'moonwalking' which was a backwards-moving digging with the feet action that resembled the dance move by that name made famous by Michael Jackson. We also recorded object manipulation (including the object manipulated and in what way), instrumental object manipulation, and attempted instrumental object manipulation. We characterized as attempted instrumental object manipulation events in which the pig held a branch sideways in its mouth, or attempted to manoeuvre a branch into this position, and made circular motions with its head, but failed to move any soil either due to a poor grip or an inappropriately shaped branch. We also recorded agonistic behaviours such as chasing, biting, and threatening, play interactions including a description, and we recorded locomotion (walking, running) and its direction. For the ethogram used in this study see [Table 1](#).

#### Results, part 3

Although our dataset of instrumental object manipulation events and nest-building sequences is not large enough for statistical analysis, several clear patterns stand out regarding who performs the observed instrumental object manipulation and



**Fig. 4.** Schematic representation of the position of tool use within a typical nest-building sequence. This representation does not indicate the fact that the four pigs were not always carrying out the same behaviour at the same time after step 1. It also does not represent that the pigs were often building more than one nest simultaneously. Following the third step, all the steps were repeated with no apparent order or endpoint.

in what context. Here we provide quantitative and qualitative descriptive data.

We observed 9 nest-building sequences. Up to four nests were being constructed at a time. When there was more than one nest site, individuals often switched the locus of their behaviour between nests as one or the other drew their attention, sometimes removing material from one partially-built nest to build the other. Once nest-building behaviours were initiated, all individuals took part but their behaviour did not always appear to be goal-oriented. For example, during nest-building Billie, and others, often collected and removed leaves from the nest rather than putting them in the nest. They may have assessed these leaves as unsuitable for the nest, but as the removed leaves were sometimes put into another nest, or the same leaves that were placed in the nest by one individual were removed by another (usually Billie), it at least appeared that they did not all share the same criteria and/or goals related to nest building.

Though complex, nest-building sequences were not random. We did not observe a nest-building sequence in the absence of leafy branches or dry leaves. The appearance of leaves near the beginning of the observation session usually led to collecting and carrying around of the leaves, and performing playful actions with the leaves such as tossing the head and twirling while holding leaves in the mouth, or shaking the leaves in another individual's face, although these actions only led to nest building in the 9 cases we observed. Digging with the nose and bringing leaves were always the first and second steps of nest building sequences. Digging with the nose in the nest was the first nest-building action in 6 out of nine episodes, and bringing leaves to the nest was the first action in 3 out of nine episodes. The third step, moonwalking, always occurred after digging and leaf carrying. This third step was initiated by Billie 6 times. This resulted in building up the walls of the nest from the outside. These three nest-building actions were then combined as nest building progressed, with no apparent coordination between individuals or evident end-point (Fig. 4). Billie in particular often interfered with the females' nest building behaviours due to his dominance. We observed several times that they waited for him to finish digging in the nest while holding leaves in their mouths, standing in what appeared to be his blind spot or out of his range until they could approach the nest and place the leaves in it.

Branch, bark and leaf manipulation events were common. 49 manipulation events or sequences were recorded for Antonia, 47 for Beatrice, 26 for Priscilla, and 14 for Billie. This category included

**Table 3**

A = Antonia, one adult female offspring. B = Beatrice, the other adult female offspring. P = Priscilla, the mother. > indicates "dominates". = indicates an ambiguous interaction without a clear winner or dominant party.

Agonistic interaction outcomes			total
A > B	B > A	A = B	18
3	3	12	
A > P	P > A	P = A	
3	2	7	12
A > Billie	Billie > A	A = Billie	
1	6	1	
B > P	P > B	B = P	15
7	0	8	
B > Billie	Billie > B	B = Billie	
2	10	0	12
Billie > P	P > Billie	Billie = P	
12	0	1	

principally collecting and carrying a large number of leaves and leafy branches in the mouth, arranging them in a nest, holding a stick in the mouth while performing another action, breaking a branch against a hard surface, tossing the head while holding leaves in the mouth, and shaking leaves in another individual's face.

We observed 7 distinct instrumental object manipulation events, all by Priscilla, the mother. These occurred during two different nest-building sequences, and in both cases after the first moonwalking event. We also observed 7 possible instrumental object manipulation attempt events, 4 by Antonia, 1 by Beatrice and 1 by Priscilla. These attempts occurred over 4 nest-building episodes, one of which was also an episode when Priscilla also successfully used a stick to dig. These attempts also uniformly occurred after moonwalking had taken place.

We observed a total of 78 agonistic interactions between the pigs (Table 3). By simple vote-counting of interactions and their outcomes it would appear that Billie, the male, dominated the three females, and the offspring Beatrice dominated her mother Priscilla. The offspring Antonia appeared to be on equal terms with both Beatrice and Priscilla. Antonia and Beatrice had the largest number of ambiguous and aggressive interactions between each other, while Antonia and Billie had the least.

We could not determine whether there was a preference for any of the spatula designs, across spatulas or between individuals, since only two of the instrumental object manipulation digging events involved a spatula: Priscilla used spatula 1 twice on the first day of observations. The other instrumental object manipulation events and instrumental object manipulation attempt events involved different sticks and pieces of bark in the enclosure. The spatulas frequently went missing, and it was not clear if the pigs had "collected" them in their hut or if they had been buried accidentally.

### Discussion study 3

These observations confirm that instrumental object manipulation is context-specific, carried out only after step 3 in the nest building sequence; mainly carried out by a single individual, both the eldest pig and also the least dominant female; and not sensitive to object form or identity.

### General discussion

We argue that the observed use of bark, sticks and spatulas for digging fits the definition of tool use provided by St Amant and Horton (2008) because it involved the manipulation of an external object (bark, stick, or spatula), it occurred exclusively and regularly within a goal-oriented repeated action pattern (digging a nest pit), and as its end result it altered both the distribution of the soil (to make a pit) and the physical properties of the tool user (a physical



disposition, digging action) and thus likely also included information transmission to the tool user in the form of proprioceptive feedback different to that without tool use. By fitting these categories including both aspects of the and/or condition proposed by St Amand and Horton (2008), the reported behaviour fits their definition of tool use. While the fit to this definition was evident from the beginning (providing the motivation for the study), having now amassed enough observations to ensure that the observed behaviour was not a fluke or mistaken observation, for the rest of the paper we will thus refer to it as tool use.

Very little is known about the behaviour or ecology of Visayan warty pigs in the wild in the Philippines, including whether tool use is a naturally-occurring behaviour in this species. The zoo context may have affected the learning and innovation potential of the pigs in this study in unknown ways (e.g. Haslam, 2013). The occurrence of several adult tool-using individuals in this one location, with no other reports from other locations, allows three possible explanations. First, it is possible that all Visayan warty pigs manipulate sticks in this way as part of their innate behavioural repertoire. We could account for previous non-observation of this behaviour in captivity if Visayan warty pigs are usually deprived of bark and sticks in their zoo enclosures and so are not able to perform the behaviour at other zoos; this does not appear to be true. Alternatively, if the behaviour is naturally performed at a very low rate it might have escaped observation until now. It would be, however, rather unusual for an apparently ineffective and sometimes poorly executed behaviour to be innate, unless the actual end result or goal of the behaviour is not what it appears to be *prima facie* (we discuss the issue of effectiveness, functionality, goals and end results below). Rather, this pattern of observations is more consistent with innovation and learning, since different mechanisms of learning can themselves result in partial or degraded transmission of behaviours (e.g. failure to learn effective object manipulation actions, failure to learn the goal). Thus a second possibility is that Priscilla, who was born in Apeldoorn Zoo, could have learned it from another pig there and transmitted it to the others at the Ménagerie. This cannot be ruled out, but given the frequency of exchange of Visayan warty pigs among the EEP zoos for breeding purposes, one might expect a pre-existing socially transmitted behaviour to have been observed elsewhere. The third possibility is that the observed tool use is an innovation of one of the pigs at the Ménagerie that spread to the others, as we explain next.

If the observed tool use is an innovation at the Ménagerie, we cannot know who originated it. However, we can assume that the transmission of the behaviour was either vertical, from mother to daughter, or horizontal, between adult females and to the adult male, Billie (Reader, 2003). It may be unlikely that Billie originated the innovation, since his observed attempted tool use during Study 2 was particularly inept. Frequency of tool use, highest for Priscilla, would not appear to be related to frequency of object manipulation in general, which was highest for the two adult female offspring—although without enough data to run robust statistical tests, we must caution that this numerical non-relation may not be robust. It also does not appear to be the case that tool use is related to frequency of nest-building behaviours, since all four individuals participated actively in all observed nest building episodes. However, we note that the primary tool user is the most subordinate member of the group (Priscilla), with the most apparent tool-use attempts made by the second-most subordinate member (Antonia). In studies of innovation in other species, subordinate individuals are most likely to develop innovations, which spread slowly to more dominant individuals (Reader, 2003). Taken together, these observations suggest that the tool use behaviour may be an innovation of Priscilla. The collection of a larger data set amenable to statistical analysis would allow us to assess this claim quantitatively.

Although we were not able to observe any original innovation of the tool use behaviour, we can speculate on its behavioural origins. We noted a head-tossing motion that the pigs use when holding leaves or leafy branches in their mouths in an excited state. This is similar to the motion used to perform the rowing movement used to dig with the stick or spatula. This excited head tossing while holding leafy branches could thus be the origin of the tool-use behaviour. This could represent a case of ritualization of the behaviour, especially if, as we speculate below, the observed tool use behaviour does not have the function or intended function that is most obvious (i.e. it contributes to rearranging the soil) but rather a function related to signalling or information transmission.

Tool use was not observed in the majority of observed nest-building episodes, even when a spatula or other potential tool was visible in the enclosure. It is notable that digging with a stick or spatula never occurred at the beginning of a nest-building sequence, even though digging with the nose or feet was typically the first behaviour to appear. This suggests that tool use, which had a digging effect, was not a substitute for other digging behaviour. We speculate that the proprioceptive information feedback to the user of using a stick to move soil may itself be the reward that supports repeated tool-use behaviour, rather than increased digging efficacy, since indeed none was apparent. In this sense, the observed behaviour might be closer to the cultural behaviours observed in chimpanzees such as the hand-clasp, play-start or branch-clasp that have no clear functional advantage (Whiten et al., 1999). In any case the tool use had a specific placement in the behavioural sequence of nest building, after step 3. We therefore think of the observed tool use behaviour as being functional, contributing to an end-result, or goal-oriented, in the sense that it has a definable position within the functional sequence of nest-building, and has a role in the goal or end result of nest-building. Whether the tool use is, when considered in isolation, a functional, goal-oriented behaviour, and what its end result should be understood to be, is discussed next.

If the observed tool-use behaviour is less efficient at moving soil than rooting but may have some other functional outcome, or is non-purposeful (Huffman and Quiatt, 1986), what maintains its performance—can it be adaptive? One argument is that it is not the tool-use *per se* that needs to be adaptive, but rather innovation capacity. This, however, leads to the argument that innovation capacity can only be adaptive if innovations are usually adaptive. If Suidae have the capacity to innovate, why not innovate a clearly adaptive behaviour? There are several possible answers to this conundrum. First, the observed tool-use behaviour is, perhaps, not adaptive, but also not maladaptive. It occurs within a larger goal-oriented, functional, purposeful, adaptive behaviour, which is nest building. Thus, if it does not disrupt, counteract, or undermine nest building, it may simply have a neutral effect. The energetic or other costs involved in carrying it out, although they may have no benefit, may have a cost that is too small (e.g. due to the very small amount of time and energy dedicated to it) to significantly impact the nest building sequence or the broader fitness of the pigs. Why, in this case, perform the behaviour? One perspective, as we suggested above, is that the pigs are motivated to carry out the tool use behaviour because they may be rewarded to perform the behaviour by the particular proprioceptive feedback it provides, which for some reason may be experienced by the learning system in the brain as a reward (it ‘feels good’). In this case, the body receives short-term feedback information generally correlated with doing something adaptive (reward), which accounts for the persistence of the behaviour until any fitness cost would remove it from the population. Equally, the observed tool-use behaviour may be maladaptive in some unknown way, but perhaps the zoo habitat buffers the pigs from the associated costs—thus, it is possible that this could only ever occur in a zoo. Secondly, the observed behaviour may

be a degradation, either due to physical incompetence, poor social transmission, inappropriate tools or substrate, etc., of a functional and adaptive digging behaviour that to our knowledge has not been observed. It might, in this case, be described as nonfunctional and either nonadaptive or maladaptive (with the same caveats as mentioned above). Thirdly, the observed behaviour makes a functional contribution to nest building and is adaptive, but in a way that we have not grasped. For example, the purpose or function of the use of the tool to dig may not have anything to do with its efficiency at rearranging soil, which appears *prima facie* to be its end result. It might, for example, if we can be allowed to speculate here, be an incipient digging movement ritualized as a signal of having arrived at a particular step in the nest-building sequence and have the effect of signalling and perhaps improving nest-building coordination among the pigs. Unfortunately our dataset cannot distinguish between any of these possibilities, and resolving this evolutionary conundrum goes well beyond the scope of this study, as it would presumably require comparative studies of the fitness of pigs with and without this behaviour in nature.

If we had definitively determined that the observed tool use was nonfunctional, would this imply that it could not be tool use? As we already indicated, we believe that the observed behaviour fits the definition of tool use given by St. Amant & Horton (2008). Correctly, they do not state that “the goal of (1) altering the physical properties of another object, substance, surface or medium” needs to be achieved in a particularly efficient or effective way, or indeed achieved at all—the behaviour just has to have this goal, to the extent that goals can be understood. As we discuss in the previous paragraph, the observed behaviour could even not have (at any time in evolution, or just currently) the rearrangement of soil as its goal, but still count as tool use by qualifying under (2) transmission of information. Or, the behaviour may have different functions for different users: if the tool use is innovated and social transmitted, the innovator may have had one goal (e.g. movement of soil), but as the innovation is not very effective, a different goal may have been attributed to it by subsequent learners (e.g. obtaining rewarding proprioceptive feedback, signalling something). This could result in a process of behavioural ritualization, which effectively might be still ongoing. Indeed, behaviours can have multiple functions, but without controlled laboratory experiments, it can be difficult to separate and validate these.

Finally, having raised the possibility that the tool use could be nonfunctional or nonadaptive, might we conclude that it is actually just a captivity-induced stereotypy that happens to have the form, but not the function, of tool use? The answer is clearly no. Stereotypies are invariant repetitive behaviours carried out for considerable periods of time, generally internally motivated rather than cued by an external event, and with a constant intensity and often rhythm, such as pacing or running along a circuit, jumping, doing flips, chewing objects, and so on (Mason, 1991). None of the observed object manipulation behaviours carried out by the pigs in this study involved invariant repetitive motions. The observed tool use was extremely rare, and occurred within a clear functional context and in response to an external event—a particular stage of nest building. It has none of the characteristics of a stereotypy. This can be clearly observed from the included video evidence.

Nest building generally started with digging in the nest, incorporated leaf arrangement to line the nest, and finally incorporated moonwalking to build up the walls. Although these behaviours were added sequentially at the beginning of nest-building sequences, there was otherwise very little structure to the nest building sequence and little evidence of coordination between the individual pigs. This may be due to an incompletely developed motivational state on the part of the females and/or the male, which might be the case as none of the females were pregnant. Since there are no reports of nest-building in Visayan warty pigs from the wild,

we have nothing to compare it to. Nor are we aware of any other reports of collective nest building in pigs.

Since it is reported that adult male *Sus cebifrons* do not normally participate in nest building despite living year-round with females (Przybylska, 2014), it is surprising that the adult male Billie performed aspects of the tool use behavior as well as participating in leaf collection, layering of leaves in the nest, and moonwalking. Adult males presumably lack the elevated hormonal levels that have been described as a releaser for the nest building action program (Arey et al., 1991), although Billie is treated with male birth control, which affects his hormonal expression. The genes controlling both male and female sexually dimorphic innate action patterns are found in both males and females, but expressed differently (Manoli et al., 2006; Xu et al., 2012). Male social learning of female-specific behaviours and novel behaviours inserted in female-specific behavioural sequences, could be an interesting case of the role of experience in modifying gene expression (Rampon et al., 2000), which could be further studied in Visayan warty pigs since the males of this species uniquely live year-round with females.

Our observations of tool-use in *Sus cebifrons* provide rare novel observations of fully unprompted tool use in a phylogenetic family in which it has not yet been recorded. Our observations open fertile new ground for research on tool use and social learning in Suidae.

## Author contributions

MR-B collected data, contributed data analysis, and wrote the manuscript. TN and LC collected data, carried out and data analysis and contributed to the manuscript. AB supervised LC and contributed to the manuscript.

## Acknowledgements

MR-B was a visiting researcher at the Musée National d'Histoire Naturelle in 2016. She is grateful to Museum staff for putting her in touch with the Ménagerie staff in order to organize the study.

## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.mambio.2019.08.003>.

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